

To boldly go where no mollusc has gone before: Personality, play, thinking, and consciousness in cephalopods*

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Abstract: The study of molluscan behavior offers intriguing possibilities and promising results, although focused mainly on coleoid cephalopods. Octopuses in particular have enduring individual differences in reactions that are strong enough to be called personalities (Mather and Anderson 1993). Given a floating or manipulable object, octopuses do not always habituate to its presence but may instead perform simple object play (Mather and Anderson 1999). One can argue they have basic concept formation, both in assessment of complex sensory information and choice of motor output. Sutherland's (1963) series of tests on octopus shape discrimination revealed that octopuses had no simple rules but were instead learning what to learn. Anderson and Mather (2007) found that octopuses chose one or more of three methods to penetrate clam shells. Each method used a different effector and prey orientation, all while the clam was under the arm web and thus visual information was unavailable. These different aspects of behavior all indicate cephalopods may have a simple 'primary consciousness' (Mather 2007), integrating perception and learned information with motivation to make decisions about complex actions. Such a conclusion offers new possible directions for the study of molluscs.

Key words: octopus, behavior, cognition

Behavior is often studied in molluscs to understand some other aspect of their functioning, not to evaluate and deconstruct the behavior itself. Behavior is, thus, seen as the consequence of physiology or structure, as in Chase's (2002) book on the behavior of gastropods and its neurophysiological foundation. Alternately, behavior may be evaluated as the outcome of evolution and the one best fit to survival and reproductive success, through foraging strategies (Stephens and Krebs 1986) or sexual selection (Dugatkin 2004). All these approaches are useful, but behavior is a valid field of study on its own, and its study can be based on Tinbergen's (1972) four areas of causation, development, evolution, and function.

Although behavior is emphasized only in the cephalopods—and its complexity revealed—the viewpoint could spread to all molluscs. Behavior is often studied in the coleoid cephalopods because of their learning capacity and high brain-body size ratio (Packard 1972) that is larger than in fish and some birds and approaches that of mammals. They also have excellent visual acuity (Gleadall and Shashar 2004), with eyes convergent to those of higher vertebrates. Cephalopods are well known for variability of behavior, and research (reviewed in Wells 1978) established their excellent learning ability and two storage areas in the brain for visual and chemo-tactile, learned information. Despite criticism of this early research (Boal 1996), the basic findings stand.

Hanlon and Messenger (1996) collected information from a wide variety of areas, but focused on body patterns and responses to predators, in reviewing cephalopod behavior.

Advances in all four areas of behavior have given molluscan specialists the opportunity to ask new questions. Development of behavior has been barely touched on, partly because many molluscs, including cephalopods, are small and planktonic at hatching. Several authors (Messenger 1968, Chichery and Chichery 1992a, 1992b, Dickel *et al.* 2000, Darmaillacq *et al.* 2006) have done developmental research on *Sepia officinalis* Linnaeus, 1758 and are reviewed in Mather (2006). Behavioral causation has been studied in learning (Wells 1978), but evolution and function have been studied only in the context of sexual selection in squid (Hall and Hanlon 2001, Jantzen and Havenhand 2003) and foraging strategies of octopuses (Ambrose 1984, Hartwick *et al.* 1978, Mather 1991a, 1991b, Vincent *et al.* 1998). The study of animal behavior is becoming both wider and deeper as researchers learn more, and this should cause malacologists to see the multiple bases of their animals' behavior. West-Eberhard's (2003) masterful combination of evolution, inheritance, environment, and development is one example. Bekoff *et al.*'s (2002) focus on cognition from the animal's own perspective and Baars' (1994) theory of a global workspace as a foundation for simpler consciousness available to non-human species are others. Some abilities that were pre-

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viously thought of as the sole domain of humans, such as tool use (Beck 1980), play (Burghardt 2004), personality (Gosling 1999), and consciousness (Edelman *et al.* 2005) are being evaluated for non-humans and not just in primates. Such assessments of cephalopods are the subject of this paper.

Personalities

Individual differences, similar to behavioral syndromes (Sih *et al.* 2004), have recently been rediscovered. The focus on species or group-specific behavior during the second half of the 20th century, both from ethological observation and assessment of learning, was an important and productive advance. Yet in the process, the individual animal was forgotten, and variation among individuals was seen as mostly noise. Although alternative Evolutionary Stable Strategies began to be recognized through game theory (Maynard Smith 1982), this work focused on small groups and not on the individual. However, psychology has a long tradition of looking at individual personalities of humans. Ideas developed in this area, especially theories such as Freudian identity or conflict with one's parents, were not easily transferred to non-human species with quite different experiential bases. Still, Cattell's (1965) factor-analytic approach offered a relatively theory-free evaluation method, using the assumption of individual temperaments. He felt young individuals had a genetic inheritance which combined with environmental pressure to shape personality. Gosling (1999, 2001) has extended this approach to animals, integrated it with research on humans, and this can be applied to cephalopods.

Personality research uses a different experimental paradigm than the usual study for differences among groups as a result of experimental intervention and controls. Instead, we tested 44 individual *Octopus rubescens* Berry, 1953 in three common situations in everyday life: (1) alerting by our opening the aquarium lid, (2) threatening by touching the animal with a test-tube brush, and (3) feeding with a live shore crab (Mather and Anderson 1993). These interventions resulted in nineteen common behavioral responses that were then sorted by factor analysis and principal components analysis to find common behavioral combinations. The result was three temperament or personality dimensions, which were labeled activity, reactivity, and avoidance for their common characteristics. Positions of individuals on these dimensions were stable across time and surprisingly similar to dimensions found both in humans (Buss and Plomin 1986) and across many animal species (Gosling 1999).

Follow-up studies on the development of temperament in another species, using 37 individuals of *Octopus bimaculatus* Verrill, 1883, were even more interesting. Sinn *et al.* (2001) followed the development of individual differences through the first nine weeks of octopuses' lives, a significant

period, as their life span is one year. Fifteen common behaviors were used in the analysis and four factors (Arousal/Readiness, Active Engagement, Aggression and Avoidance/Disinterest) were isolated. As expected if inheritance had a significant effect on temperament, the developmental trajectories of octopuses from the same brood (at least 50% related to one another) were similar. Behavior still showed clear changes across the study, regardless of brood membership. No experimental manipulation was done to alter the environment, as the tiny animals were each kept in a small, barren chamber. A fascinating study would be to see what a stressful early life would do to form the developing personality of the young octopus.

A third study of cephalopod personalities (Sinn and Moltschaniwskyj 2005) used the sepiolid squid *Euprymna tasmanica* Pfeffer, 1884, which has the advantages of having a short five to eight month life span, small size, and solitary habit. This species had four enduring traits: Shy/Boldness, Activity, Reactivity, and Burying Persistence (bury into the soft sand substrate to avoid predation). Unlike in the octopuses, these traits were situation-specific so that activity in the threat test, for instance, did not correlate with that in the feeding one. Also, sex did not affect personality scores although maturity stage did. Fully mature squid were more Threat Active and more Threat Bold as well as less Feed Reactive. This change, in a semelparous species, may reflect a switch from a focus on somatic growth to a short lived concentration on reproduction (Rocha *et al.* 2001). Behaviors in antipredator situations were heritable, while those in feeding ones were not (Sinn *et al.* 2006), and female boldness in foraging explained a small but significant amount of variation in brood hatching success. The convergent results with the studies on octopuses support the idea that relatively stable dimensions of personality may be a characteristic of the cephalopod group.

Play

Many animals react to their environment not by simplistic responses to conditioned stimuli behavior but by exploration, which involves active extraction of information from the surroundings (Hutt 1966). Given a complex environment, many animals will explore and then, as stimuli are repeatedly presented, will habituate to them (Baldwin and Baldwin 1986) and cease to respond. Yet sometimes an animal will instead turn to interactions that are more wide-ranging; Hutt (1966) suggested that orientation changes from 'what does this object do' to 'what can I do with this object?' Play is often defined as simple behavior having no immediate benefits, including repetitive or exaggerated interactions out of sequence compared to normal activity (Burghardt 2004). Play has been considered a human characteristic but is also present in many, though not all, large-

brained mammal species (Iwaniuk *et al.* 2001) and sometimes in birds (Diamond and Bond 2003) and is useful for acquisition of adult behavior by altricial young in the protective care of their parents. So why should octopuses play? Possibly because they have manipulative, flexible arms (Kier and Smith 1985, Mather 1998) and thus researchers can recognize and categorize their actions and trace brain capacity for learning (Wells 1978) about the complex subtidal environment in which many octopus species live.

Object play is thought to be expressed when an animal is safe from the danger of predation and when items can be manipulated. We gave *Enteroctopus dofleini* (Wülker, 1910) at the Seattle Aquarium, empty pill bottles weighted to float just at the air-water interface (Mather and Anderson 1999). The tank included a slow water current. Eight octopuses were given ten trials, each lasting until the animal made no contact with the bottle for 30 minutes. Octopuses habituated within trials, spending less and less time in contact with the pill bottle. However, across trials, the situation was quite different as latency to contact and duration of contact with the stimulus did not decrease. Possible play with the object occurred in two of the animals. Each octopus jetted water at the floating bottle until it passed to the far end of the tank and waited until the current returned it to repeat the activity, which resembled bouncing a ball, over 20 circuits in each case. This behavior was different from repulsing the jar, by holding it away with 1-2 suckers on an extended arm.

The form this play behavior took was surprising, causing me to ask why there was not manipulation with the arms? One possibility is that the arms, with 2/3 of the animals' neurons, are under local rather than central control (Rowell 1963, 1966) and that information about the output they produce is not centrally monitored. Local control of pre-programmed responses (*e.g.*, an autotomized arm can walk) might make it more difficult for the arms to produce playful behavior. Another possibility is that the control of the water jet output, which originates from the circulatory system and is used for respiration, is more available for shifts in behavior. Octopuses use jet propulsion for swimming through the water (Wells 1990), though not with the efficiency of the open-ocean squid (O'Dor and Webber 1986). The octopus jet is also used to clean out potential homes (Mather 1994), to excavate clams from the sand (High 1976), and to repel scavenging fish from the remains of prey in the midden outside the home (Mather 1992). This flexibility represents an important characteristic of higher non-stereotyped behavior, defined as using a behavior in a quite different situation (Hirschfeld and Gelman 1994). Perhaps jetting was a behavior that was simply available.

Further investigation of play-like behavior suggested it is a wider phenomenon in octopuses. Kuba *et al.* (2006) tested *Octopus vulgaris* Cuvier, 1797 with presentations of

plastic blocks, clam prey, and empty clam shells. The octopuses ate the clams, ignored the empty shells, and sometimes engaged in play-like behavior with the blocks. The play behavior consisted of passing the block from arm to arm, extending the arm and pulling it back near the body, and pulling the block along as the octopus moved. These were designated only play-like on the basis of numbers of repetitions. The arms were clearly central to the actions, and the peak of playful behavior came during the sixth of ten trials, after which the octopuses habituated again. Interestingly, Kuba *et al.* (2006) found that, unlike in mammals (Fagen 1981, Power 2000), young and adult octopuses played the same amount. For the solitary octopus, play was not the result of needing to learn the nuances of a social group, nor was it restricted to the protected environment of the family. It did not occur frequently but occurred equally at different times in the lifespan.

Was this an exception, or will playful behavior be confined to the relatively large-brained and exploratory coleoid cephalopods, perhaps just to the octopuses with their large repertoire of arm actions (Mather 1998)? Do animals have to have a large brain to play? Anecdotal evidence of playful behavior in invertebrates includes snails rising in an aquarium holding on to bubbles, then sinking to the bottom and rising again (Burghardt 2004). One reason we were able to identify play in the octopuses was its similarity to behaviors that playful children perform (*e.g.*, bouncing a ball). Knowledge of the behavioral repertoire of most molluscs is so limited that out-of-sequence and fragmented behavior would usually go unrecognized. How could researchers discriminate play of sea hares, scallops, or nautilus? Perhaps this is why it has been characterized only in an octopus.

Thinking

Outside of the reflexive behaviors expected of invertebrates lies the whole area of learning, including concept formation, problem solving, and thinking, once thought the domain of primates but now identified in different species, contexts, and adaptive situations (Bekoff *et al.* 2002), including for corvid birds (Emery and Clayton 2004). With capacity for learning from visual and chemotactile stimuli (Wells 1978, Mather 1995), octopuses seem to have the potential for such types of cognitive ability. Yet, in standard indices of accomplishment like Thomas' (1980) levels of learning, octopuses have not shown high scores. Using visual discrimination, octopuses perform reversal learning (Mackintosh and Mackintosh 1963) and attain Thomas' (1980) Level 5, but did not learn the concept of oddity (Boal 1991) to accomplish Level 6. However, ecological constraints rather than learning capacity may be impeding them. Octopuses have great difficulty sustaining the criterion of eight of ten correct responses in continued trials (Papini and Bitterman

1991) used for vertebrates. This may be adaptive since field studies (Mather 1991a) show that they are “win-switch” foragers (Stephens and Krebs 1986), and sampling the unrewarded stimulus or area is useful rather than maladaptive. When a crab is removed from under a rock or a clam dug up from the sand, another will not reappear the next hour or day, and the octopus needs to explore different areas. More ecologically meaningful situations, such as using spatial memory for navigation (Boal *et al.* 2000) as has been demonstrated in their natural environment (Mather 1991b), may be a better test for octopod cognitive capacity.

Nevertheless, there are laboratory situations where octopuses show concept formation, if a concept is defined as abstractions that make it possible for animals to solve novel choice problems without prior experience of the specific exemplars offered (Gould 2002: 43). In a series of experiments on visual shape recognition, Sutherland (1963, also see Wells 1978) hoped to understand what he called the rule of shape discrimination by the octopus visual system, using paired stimuli where the octopus was given a reward for touching one and punishment when touching the other. He found that octopuses could discriminate vertical vs. horizontal extensions of the shape, as in mammals (Matlin and Foley 1997), which are also less competent at discriminating oblique orientations. However, octopuses could also use another rule to discriminate a figure with the same extent on these dimensions but differing in edge-to-area ratio. They could tell a square figure from a circular one of the same dimensions, perhaps by angular changes, and could discriminate the same figure rotated 90 degrees. Sutherland extended six hypotheses about what stimulus dimension the octopus was using to evaluate a figure, but Muntz (1970) produced figures that octopuses could discriminate that did not differ on any one of these. In short, octopuses did not have a single, simple rule for encoding visual shapes but instead chose the correct one for each test. This ability was also shown in Messenger and Sanders' (1972) study, where octopuses trained with two valid cues discriminated faster than those given only one. Octopuses using one cue took longer to transfer to a situation where the other was the relevant one (Mackintosh and Mackintosh 1963). They were learning what aspects of the stimulus were important.

With a variety of techniques to penetrate clam shells, octopuses may also show simple concept formation using chemotactile cues. They use simple trial-and-error learning for the appropriate penetration method (McQuaid 1994, Fiorito and Gherardi 1999, Steer and Semmens 2003), trying to pull the clam valves apart and then switching to the more time-consuming drilling through the shell if necessary. Anderson and Mather (2007) noted that *Enteroctopus dofleini* used different tactics on different clam species, pulling apart the weaker manila clams, breaking the fragile mus-

sels, and drilling or chipping the valve edge of the stronger little neck clams. When manila clams were wired shut, octopuses switched to drilling or chipping. Given intact clams, they ate least of the little neck clams but they preferred this species on the half shell; the excess effort to open the shell overrode their prey preference. Different areas of the clam valves were contacted for each technique, so the octopuses must have switched shell orientation from umbo-to-the-mouth for arm pulling to a lateral presentation for salivary papilla drilling (which was preferentially over the adductor muscles or the heart) or anterior or posterior-to-beak for chipping. Three techniques using three different effectors (arms, salivary papilla, or beak), and three prey positions were all used in the correct combination without access to visual information. Without observation inside the arm web, it is difficult to know if this is simple trial-and-error learning, but the combinations indicate that it is more.

Are such manipulations of information within the capacity of only the coleoid cephalopods within the molluscs? In general, other molluscs have been studied as if such capacities did not exist, and there is excellent information about reflexive behavior and its neural control in the sea hare, scallop and sea slug, for instance. However, Chase (2002) provides some information about the complexity of gastropod behavior that would be an excellent place to start. Owl limpets defend territories on the rocks (Stimson 1970), and other limpets occupy scars for home sites fitted to their own shell for up to three years (Hodgson 1999). How is this behavior controlled? Sea hares migrate long distances (Hamilton 1985), under control of what stimuli? Several gastropods have complex escape responses triggered by the saponin in seastar tube feet (Bullock 1953) and no extensive study of this behavior has been carried out. The authors of chapters in Prete's (2004) book explore examples of flexible, adaptive behavior in other invertebrates, such as color vision of honeybees, prey capture in spiders, and visual recognition in mantis shrimp. Animals can do a lot with simple nervous systems, and molluscs are no doubt among them.

Consciousness

The set of behavioral traits described above suggest that octopuses have a simple form of consciousness. Primary consciousness can be defined as “a reportable multimodal scene composed of perceptual and motor events” (Seth *et al.* 2005: 120) and is sought for in non-human animals. Of course, some theorists argue that no such emergent systems exist, and Gould and Gould (1994) caution against assuming complex cognition where a chain of simple behaviors might be the cause. However, others have suggested that if humans have higher-order consciousness, then homology indicates that non-human vertebrates might have a simpler form. Evidence might be neural, particularly reentrant connectivity

between brain areas for perception and those involved in memory (Edelman *et al.* 2005: 170) and to a lesser extent in behavior suggesting such connectivity. As cephalopod brain physiology is still poorly known (but see Williamson and Chrachri 2004 and Hochner *et al.* 2006 for suggestions of such feedback circuits), behavioral evidence must be used primarily for evidence of simple consciousness in these animals (Mather 2007).

Such primary consciousness would be the result of an emergent central representation of the world and oneself. Shepherd (2001) discusses humans' perceptual representation of the external world, although he comments it cannot be a completely accurate one, and Gray (2004) notes that our perceptual world is largely a construct. In fact, one of the basic lessons of human perception is that we form constancies (of color, lightness, and shape) which transcend the immediately available information but make the changing world intelligible to us (Matlin and Foley 1997). Sutherland's studies suggest that octopuses were building such constancies about visual shapes, though none of the early learning studies ever used a comparison that might address this question.

Another important aspect of consciousness is that awareness is only extended to a small proportion of the information incoming from perception and outgoing to muscle control (Gray 2004). Gould and Gould (1994: 149) comment that "thinking is a potentially dangerous backup strategy, too slow and error-prone to be applied indiscriminately." Merker (2005: 98) comments on thinking and assumes its limited task is "optimizing behavioral choices in the light of diverse types of information." One area of information that researchers have assumed is not centrally calculated in octopuses and thus omitted from consciousness, as in humans, is arm movement. To control the muscular, hydrostatic skeletal system (Kier and Smith 1985), octopuses have ganglia all along the arms and above each sucker, and arm control has long been assumed to be reflexive (Rowell 1963, 1966). Recent studies (Sumbre *et al.* 2001, 2006) have confirmed arm control uses peripheral motor programs and simple output strategies in octopus arm extension. Yet Grasso's (2008) studies of the diversity of programming of sucker use challenge this view. Is such flexibility a result of the larger, more complex on-board computer represented by the arm neurons, or is central monitoring evaluating task demands and planning actions? Our mammalian heritage leads us to think of central planning as complex and peripheral as simple, but these divisions may need re-thinking for octopuses.

Baars' (1994) global workspace model of consciousness, with a short-term, attentional spotlight lasting less than a minute, might be a good model for primary consciousness in cephalopods. Merker (2005) feels that such a capacity might

arise only in mobile animals with centralized brains faced with decision making in a complex environment. The limited evidence we have suggests that cephalopods do use this kind of decision making; they are active in exploration of their environment (Mather 1991a) and of novel objects introduced to them. For example, Wells (1978) reported that the 'life span' of a floating thermometer introduced into an octopus tank was 5 minutes, and there is anecdotal evidence of similar manipulations noted by aquarium keepers. Octopuses also quickly habituate to the repeated presence of a simple object and move the attentional spotlight except when actions are transformed to play (Mather and Anderson 1999, Kuba *et al.* 2006). Such a central processor could also make decisions about prey entry techniques of octopuses for clams, since action, effector, and clam orientation all must be coordinated (Anderson and Mather 2007).

How might cephalopods' possession of personalities indicate simple consciousness? Merker (2005: 93) assumes that consciousness mediates between motivational, sensory, and motoric functions. The presence of distinct personalities in cephalopods (Mather and Anderson 1993) suggests both motivational differences among individuals and a complex base on which they act. Simple neural structures should produce more behavior that is stereotyped among individuals in the input-output relationships than what is seen in cephalopods. West-Eberhard's (2003) detailed evaluation makes it clear how adaptive plasticity allows combining of genetic influence with environmental pressure (though she had no concept of a central controller) to produce individuals, each adapted over time to its micro-environment.

The ideas advanced in this paper and a deeper evaluation of behavior *per se* can indeed take the study of molluscs in directions it has not traditionally gone. There is much to be gained by doing so: definitely a better understanding of the cephalopods, a new respect for the competence of lowly invertebrates, and new questions to ask, by extension, of all the mollusc groups.

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